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Water as a resource, stress and disturbance shaping tundra vegetation

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Abstract

Water is crucial for plant productivity and survival as a fundamental resource, but water conditions can also cause physiological stress and mechanical disturbance to vegetation. However, these different influences of water on vegetation patterns have not been evaluated simultaneously. Here, we demonstrate the importance of three water aspects (spatial and temporal variation of soil moisture and fluvial disturbance) for three ecologically and evolutionary distinct taxonomical groups (vascular plants, bryophytes, and lichens) in Fennoscandian mountain tundra. Fine-scale plant occurrence data for 271species were collected from 378 x 1 m2 plots sampled over broad environmental gradients (water, temperature, radiation, soil pH, cryogenic processes, and the dominant allelopathic plant species). While controlling all other key environmental variables, water in its different aspects proved to be a crucial environmental driver, acting on individual species and on community characteristics. The inclusion of the water variables significantly improved our models. In this high-latitude system, the importance of spatial variability of water exceeds the importance of temperature for the fine-scale distribution of species from the three taxonomical groups. We found differing responses to the three water variables between and within the taxonomical groups. Water as a resource was the most important water-related variable in species distribution models across all taxonomical groups. Both water resource and disturbance were strongly related to vascular plant species richness, whereas for moss species richness, water resources had the highest influence. For lichen species richness, water disturbance was the most influential water-related variable. These findings demonstrate that water variables are not only independent properties of tundra hydrology, but also that water is truly a multifaceted driver of vegetation patterns at high-latitudes.

Keywords: arctic–alpine, soil moisture, species distribution

Introduction

Water is fundamental for the growth, performance, and geographical distribution of vegetation. Water can be a limiting resource for vegetation, but it is also an important stress (both when excessively abundant and scarce) and causes multiple types of disturbances (such as fluvial erosion and accumulation) (Grime 1977). Individual plant species respond differently to water conditions, i.e. they have unique hydrological niches, which is an important mechanism for species co-existence within vegetation communities (Silvertown et al. 2015). In addition, water shapes species distributions and diversity across gradients from local occurrence patterns to entire biomes (Franklin et al. 2016, le Roux et al. 2013a, Whittaker 1972).

Cold regions are often considered as energy-limited ecosystems, but in a global change context, the role of water has increasingly received attention in the on-going environmental changes experienced in the tundra biome (Bring et al. 2016, Nabe-Nielsen et al. 2017). Tundra plants allocate a large part of their biomass below soil surface, where their roots are relatively shallow rooted (Canadell et al. 1996, Iversen et al. 2015). Consequently, in tundra ecosystems, most plant-available water is restricted to a thin topsoil layer as soil moisture, which is recharged by precipitation, ground-water, and meltwaters (Barichivich et al. 2014). Temporal variation of soil moisture, such as occasional water-logging and drought, exposes vegetation to physiological stress (Trahan and Schubert 2016). Furthermore, water-related disturbance posed by fluvial processes provide nutrients from the accumulation of fluvial sediments (Giblin et al. 1991). Fluvial disturbance include also water-induced erosion, which removes soil surface horizons and causes mechanical damage to sessile organisms, such as vascular plants, mosses, and lichens (le Roux et al. 2014a). These evolutionary and ecohydrologically diverse taxonomical groups are key components of tundra ecosystem and presumably have dissimilar tolerances to different water-phenomena (Iturrate-Garcia et al. 2016). Therefore, it is imperative to study how various aspects of water influence fine-scale species distributions, species richness, and community composition in the tundra.

The influence of soil moisture variation on vegetation patterns is a pronounced research gap in ecology, particularly at high-elevations and -latitudes (Crimmins et al. 2011, le Roux et al. 2013a, Silvertown et al. 2015), where climate change has greatly impacted both the hydrosphere and cryosphere (Bring et al. 2016, Fountain et al. 2012). These changes have implications for precipitation, evaporation, and snow dynamics, all of which alter water conditions experienced by plants (Barichivich et al. 2014, Winkler et al. 2016). Climate simulations project more rainfall in place of snowfall during winter, which combined with earlier snowmelt could lead to extreme drying late in summer and autumn (Bintanja and Andry 2017, Kankaanpaa et al. 2018). The increasingly variable weather conditions also affect soil moisture availability and variability (Bring et al. 2016). As

a result, soil moisture extremes (i.e. lack of soil oxygen or lack of water) are likely to become more frequent, which will also reflect on vegetation patterns (Franklin et al. 2016, Silvertown et al. 2015). Since no study has simultaneously considered the effects of water on vegetation patterns from its three ecologically-meaningful aspects – a resource (WRE), a stress (WST), and a disturbance (WDI) – this gap in our ecological understanding remains.

High-latitude ecosystems have shown slow responses to short-term experimental manipulations (Blume-Werry et al. 2016). Thus, observational studies along environmental gradients provide us with a valuable approach to investigate tundra vegetation patterns and to predict the consequences of environmental changes (Yuan et al. 2017). Here, we use an observational approach together with species distribution modelling to show how different aspects of water (i.e. soil moisture level, soil moisture change, and fluvial disturbance) influence vegetation patterns, while controlling for eco-physiological factors. We collected fine-scale occurrence data for 271 species from 378 plots surveyed in mountain tundra. In addition to the three water variables, our study setting covered all the key environmental variables (temperature, radiation, soil pH, cryogenic processes, and the cover of the dominant allelopathic plant species) that need to be taken into consideration when studying vegetation patterns from a species distribution modelling approach (Austin and Van Niel 2011, Mod et al. 2016).

Our study setting enables a robust assessment of the drivers of tundra vegetation communities, because, firstly, our study is conducted at an ecologically relevant scale, which matches the scale at which water and other factors vary and interact with the plant species (Bramer et al. 2018). Secondly, our setting spans the range of the key environmental gradients within the study system, as well as a relatively large number of species increasing the generalizability of the results (Franklin 1995). Thirdly, our field-quantified observational data comprise the main direct predictors and resource variables relevant to the species being studied (sensu Austin 1980). We determined for the first time, how significant are the roles of three different water aspects in shaping fine-scale assemblages of vascular plants, mosses, and lichens in tundra.

Material and methods

Study setting

Data were collected on Mount Saana in northwestern Fennoscandia (69°03´N 20°51´E), with biotic data collected over three consecutive growing-seasons (2011 – 2013). All abiotic data were collected in the 2013 growing-season. On average, July is the warmest and the wettest month at this site (June: 7.5°C, 42 mm; July: 11.2°C, 73 mm; August: 9.6°C, 47 mm; 1981 – 2010), as measured from 2 m above ground at the nearby Kilpisjärvi meteorological station (69°05´N 20°79´E; 480 m a.s.l.), which is located 1.5 km from the study area (Pirinen et al. 2012). The landscape is dominated by alternation of minor topographic terrain features, such as hilltops, ridges, and small depressions. In addition, there are several soil types ranging from rock outcrops, boulders, glacial till, and fluvial deposits to peat deposits. Variation in soil properties together with the fine-scale topographical heterogeneity creates a mosaic of micro-habitats characterized by, for example, fine-scale variation in soil moisture (Kemppinen et al. 2018). Most of the area is covered by a thin organic layer ranging from 0 – 70 cm in depth (Kemppinen et al. 2018). The main vegetation type of the area is dwarf-shrub heath dominated by Empetrum hermaphroditum and Vaccinium spp., and to a lesser extent by Betula nana and Phyllodoce caerulea (for species list, see Appendix S1).

Sampling design and methods

We surveyed 21 study grids on Mount Saana (Figure 1). The elevation of the study grids ranged from 595 to 810 m a.s.l., with all the grids located above the treeline (comprised of Betula pubescens ssp. czerepanovii). Each grid contained 18 study plots of 1 m² at 3 – 4 m intervals and covered a range of environmental conditions (grids were initially orientated to maximize variation in vegetation and mesotopography; see le Roux et al. 2013a). In the plots, we identified 271 species and estimated their percentage cover in all 378 plots (for taxonomy details see Appendix S1).

Soil moisture was measured on three occasions during one growing-season (June 12th to 13th; July 23rd to 24th; August 9th 2013). We used a hand-held time-domain reflectometry sensor to measure volumetric water content (VWC%) up to a depth of 10 cm (FieldScout TDR 300; Spectrum Technologies, Plainfield, IL, USA). On each sampling occasion, three measurements were taken within each plot, accounting for possible within-plot moisture variation. Consequently, the mean of the three points was used for calculating WRE and WST. To ensure comparability of measurements, each set of measurements was taken on a day, where there had been no precipitation for at least the preceding 24 hours (Bramer et al. 2018). We quantified WRE as soil moisture level (mean over the three sampling occasions VWC%), WST as temporal variability of soil moisture (coefficient of variation of the three sampling occasions [CV]) (Brown 1998), and WDI as the intensity of active fluvial processes (i.e. water-driven processes) occurring in each plot during the growing-season (for more details on the fluvial processes in periglacial environments, see French 2007). WDI was visually assessed in situ by a geomorphologist, who surveyed the percentage cover of top-soil surface affected by fluvial erosion caused by small meltwater streams as well as fluvial accumulation (i.e.

alluvial deposits) in each plot (following methods of Hjort and Luoto 2009, le Roux et al. 2014a). All surveys were carried out by the same geomorphologist, who focused only on quantifying geomorphological disturbance to ensure the independence of the vegetation and geomorphological data.

Soil temperature of each plot was measured using miniature temperature loggers (ThermoChron iButtons, San Jose, CA, USA). Loggers were buried 10 cm below the soil surface, measuring at 4-hour intervals year around. Soil temperature data were then used to calculate the growing degree day (GDD) per plot, using a threshold value of 3°C. Due to malfunctions, the records from 56 loggers were lost. For these plots, we interpolated the GDD values based on the surrounding functioning loggers using inverse distance weighting (IDW) interpolation as implemented in R package gstat (Pebesma 2004). IDW predicts values (Z) for unobserved points (S0) by calculating the weighted average of the known points (Si; Equation 1),

$$\hat{Z}(S_0)=(\sum_{i=1}^{n}Z(S_i))/(\sum_{i=1}^{n}w(S_i)), \quad (1)$$

where the weights w(Si) for observations are calculated based on their distance to the interpolation location (Equation 2),

$$w(S_i) = \| S_i - S_0 \|^{-p}, \quad (2)$$

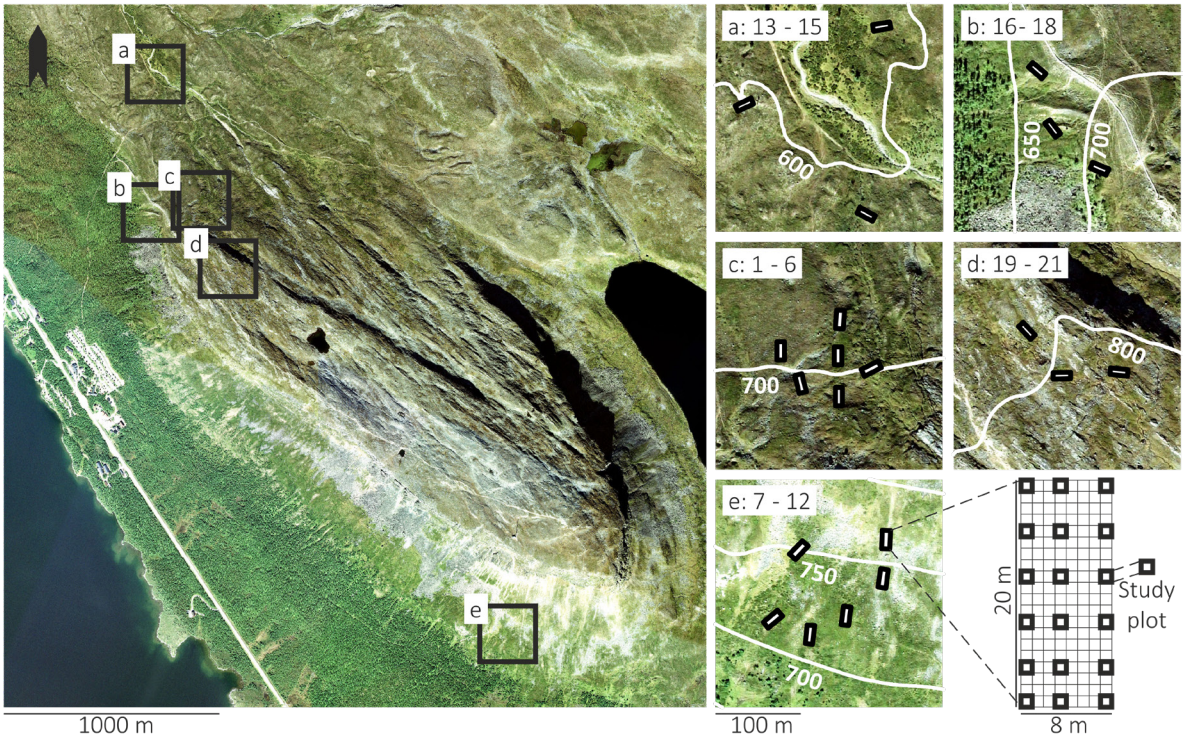
with $\| \cdot \|$ indicating Euclidean distance and p an inverse distance weighting power (Bivand et al. 2008). The optimum p for each grid was bracketed (from 0.5 to 6.0 at 0.5 intervals) to optimize Spearman's correlation coefficient (rs) between the observed and interpolated values using leave-one-out cross-validation. The cross-validation statistics over the study grids indicated a good agreement between the observed and interpolated GDD (rs = 0.81).

Solar radiation influences species distribution, as light affects several biophysical processes, such as photosynthesis (Austin and Van Niel 2011, Rorison et al. 1986). Incident radiation (RAD) was calculated as the maximum potential solar radiation per plot (i.e. assuming clear sky conditions) using field-quantified slope and aspect values of each plot (following McCune and Keon 2002). Soil pH (SpH) is an important filter of the local species pool of tundra vegetation, and it may vary strongly over short distances (Gough et al. 2000). It is an ultimate environmental driver (sensu Eskelinen et al. 2009), yet, a cost-efficient proxy for assessing nutrient availability, as soil pH alters various chemical processes between soil and vegetation (Eskelinen et al. 2009). SpH was determined from air-dried soil samples using distilled water in the process in the Laboratory of Geosciences and Geography (University of Helsinki) following the International Organization for Standardization 10390:1994 (E) protocol (see le Roux et al. 2013b). Soil frost-related disturbances affect alpine vegetation diversity, peaking at intermediate levels of disturbance (Fox 1981). As the main form of soil disturbance in our study area, we included cryogenic processes (CRY) in our analysis. CRY represents the percentage cover of cryoturbation (frost churning of the topmost soil) and solifluction (see French 2007, le Roux et al. 2014a). CRY was determined in situ following the same protocol as in WDI. To account for the effect of biotic interactions (BIO; le Roux et al. 2013b), we included the percentage cover of Empetrum hermaphroditum as a predictor variable (see le Roux et al. 2014b). This dwarf-shrub is highly competitive, both mechanically and chemically, with the cover of Empetrum per plot used as a proxy for the intensity and/or frequency of its interaction with other species (le Roux et al. 2014b). Empetrum was present in 89% of the plots, with its cover ranging from 0.25 – 95.0%. If the shrub was absent, BIO was assumed to be zero.

Statistical analysis

We investigated the effect of water-related variables on the fine-scale assemblages of vascular plants, mosses, and lichen species. Here, we used species distribution modelling, species richness modelling, and community composition analysis. We used plot-specific coverage data from all 271 species (116 vascular plant, 68 moss, and 87 lichen species) in modelling species richness and analyzing community composition. In modelling the distribution of individual species, we used presence-absence-data on a subset of 152 species, which occurred in ≥ 8 plots (i.e. occurring in ≥ 2% of plots; 68 vascular plant, 30 moss, and 54 lichen species).

We used four statistical modelling methods in the species distribution and species richness models to improve the generalizability of our analysis and to reduce uncertainties related to the choice of modelling technique (Marmion et al. 2009). We examined the relationship between predictor variables (GDD, RAD, SpH, CRY, BIO, WRE, WST, and WDI) and the distribution of individual species and richness patterns using generalized linear models (GLM), generalized additive models (GAM), generalized boosted regression models (GBM), and random forests (RF). All four techniques are able to incorporate interactions between predictors. As a non-parametric extension of linear regression models, GLM allows the use of non-normally distributed response variables (Nelder and Wedderburn 1972). GAM splits the regression lines into sections and tracks nonlinearity of relationships by using local spline smoothing functions (Hastie and Tibshirani 1987). The user controls the fitting of the smoothing function by appointing the maximum model complexity. GBM is a sequential ensemble modeling method that combines a large number of iteratively fitted classification trees into a single model with improved prediction accuracy (Elith et al. 2008). Random forest is an ensemble modelling method that generates a large amount of trees, where each tree is built



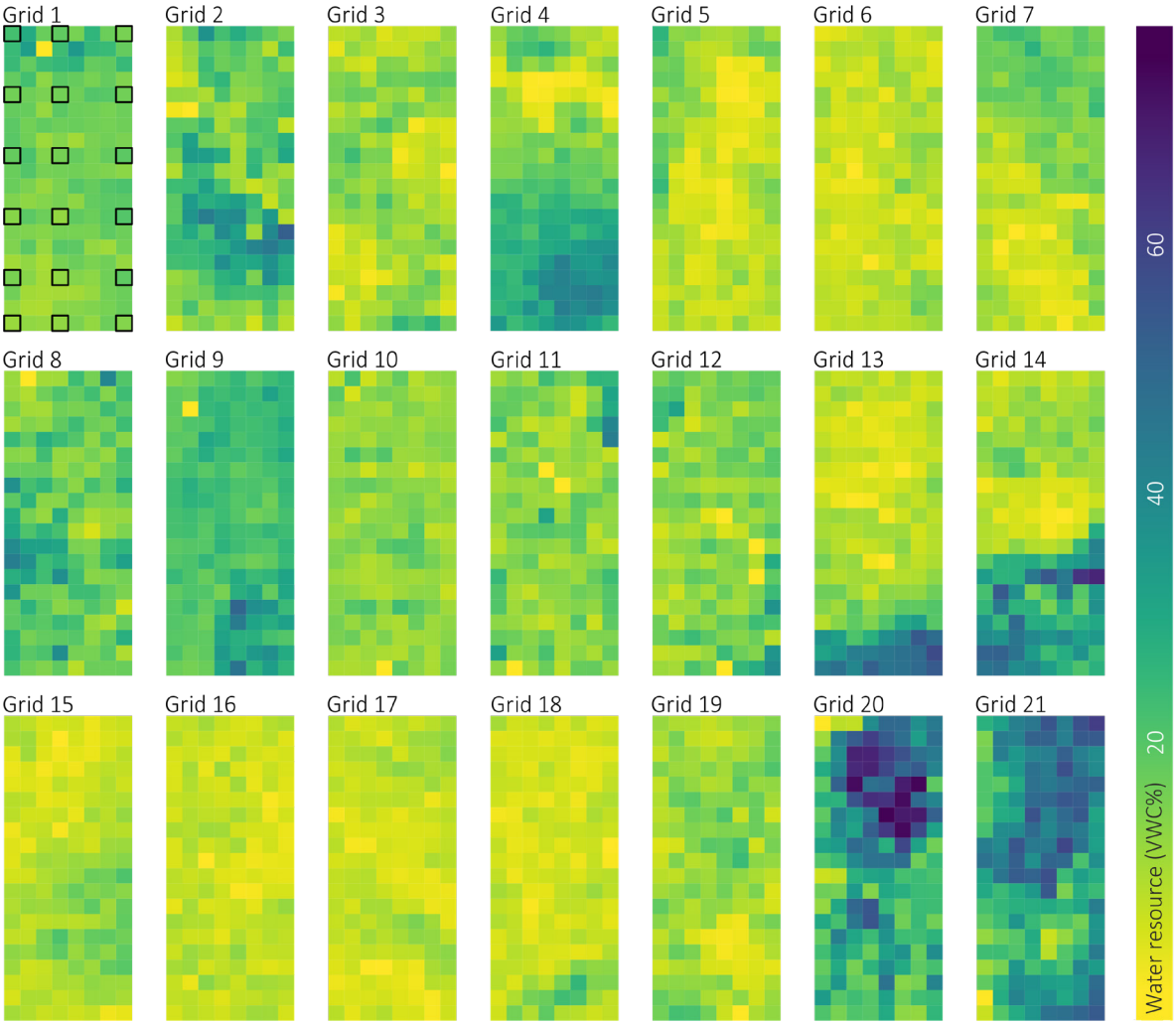


Figure 1. Study design and water resources (volumetric water content;VWC%) across the study grids. To capture the environmental gradients present within the study area, the study grids were located and oriented to sample as diverse conditions as possible, maximizing both environmental variation within (e.g. moisture, topography) and between (e.g. radiation, pH) grids. Water resources were measured within each 1 m² plot (n = 3360), although, in these analyses we used a subset of 378 plots (at 3 – 4 m intervals; bolded plots) for which observations of the three species groups and in situ measurements of all eight environmental variables were available.

using bootstrap sampling of the data (Breiman 2001). RF uses bagging where predictors are randomly selected for model calibration and the final prediction is the average over all trees in the ensemble.

Species distribution models ("distribution models" from hereafter) were run using the biomod2 R package for fitting GLM, GAM, GBM, and RF, assuming a binomial distribution for GLM and GAM, and a Bernoulli distribution for GBM (Thuiller et al. 2016). We assessed the model performance using cross-validation (random 70/30 split with no replacement) with ten repetitions. We used the area under the curve (AUC) and true skill statistic (TSS) for evaluating and comparing the distribution models. For species richness models ("richness models" from hereafter), we used the stats, mgcv, gbm, and randomForest R packages, assuming a Poisson distribution for GLM, GAM, and GBM (Liaw and Wiener 2002, Ridgeway 2017, Wood 2011). For all GAMs, the maximum degree of smoothing was initially restricted to three, which was further optimized by the model-fitting algorithm. For all GBMs, the number of trees was set to 3000, interaction depth to four, learning rate to 0.001, and bagging fraction to 0.75. For all RF models the number of trees was set to 500. For evaluating the richness models, we used 100 repetitions in cross-validation (70/30). We used the coefficient of determination (R^2) and root mean squared error (RMSE) for evaluating and comparing the richness models. For distribution and richness models, we used Wilcoxon's paired rank test for testing the significance of improvements, when comparing the base model (Equation 3) to the full model (Equation 4):

$$\text{Base model} = \text{GDD+RAD+SpH+CRY+BIO} \quad (3)$$

$$\text{Full model} = \text{GDD+RAD+SpH+CRY+BIO+WRE+WST+WDI} \quad (4).$$

We assessed the relative influence (0 – 1) of predictor variables in the models by calculating variable importance following the method of Niittynen and Luoto (2018). First, we fitted the models (all four statistical methods) with the unmanipulated data. Then, we used the models to make two predictions: one using the original data, and another using a dataset in which individual predictor variables were randomly shuffled. Then, we calculated variable importance as (Equation 5):

$$\text{Variable importance} = 1\text{-}cor_{Spearman}(prediction^{unmanipulated} \sim prediction^{shuffled}) \quad (5).$$

For species richness models, we repeated this procedure 100 times for each response variable, each predictor, and each modelling method by bootstrapping the data (random sampling with replacement). For distribution models, we repeated the procedure 10 times for each species. Since the procedure was based on model predictions, it is independent of the modelling methods.

We used non-metric multidimensional scaling (NMDS) to analyze community composition and the changes of species assemblages along environmental gradients (using the metaMDS function from the vegan package) (Oksanen et al. 2017). For examining the community composition based on all three taxonomical groups combined, we set the number of dimensions to three. The first NMDS axis (NMDS1) represents the main axis of variation within the community.

We plotted the relationship between species richness or species community composition (plot scores of NMDS1) in relation to the most important water variable and temperature , to explore how the community composition changes in relation to these fundamental factors controlling tundra vegetation. Here, the NMDS scores were calculated separately for each taxonomical group, with the potential dimensions restricted to four. GAM models fitted to the whole dataset were used to predict species richness and NMDS1 values for an artificial dataset, which consisted all possible WRE and GDD combinations. For species richness predictions, other predictor variables (other than WRE and GDD) were set as constants to their values at plot with maximum species richness (median of those, if there was more than one in a plot). For community composition predictions, other predictors were set to their median value, which were calculated based on all plots in the original dataset. Species-specific WRE and GDD optima were determined for each species as the median WRE and GDD values of all plots, in which the species was present. We used R version 3.3.2 for all analyses and models (R Development Core Team 2016).

Results

All three water-related variables showed pronounced variation over the study area: WRE ranged from 5.5 to 64.9 VWC% (mean and standard deviation: 19.6 and 11.3 VWC%), WST from 0.2 to 107.0 CV (24.7 and 15.9 CV), and WDI from 0.0 to 90.0% (3.4 and 10.6%) (Appendix S2). Pair-wise correlations between the water-related predictors were $|rs| \leq 0.40$ and between all predictors $|rs| \leq 0.55$ (Appendix S3).

Species distributions

WRE was the most important water-related variable in distribution models across all taxonomical groups (Figure 2 a-c), showing the strongest influence on the occurrences of mosses. The inclusion of the three water-related predictors improved the predictive performance of the distribution models for all taxonomic groups: AUC value increased significantly from 0.733 to 0.754 (two-tailed Wilcoxon signed rank test, $V = 7241.0$, $p = 0.009$) (for TSS values, see Appendix

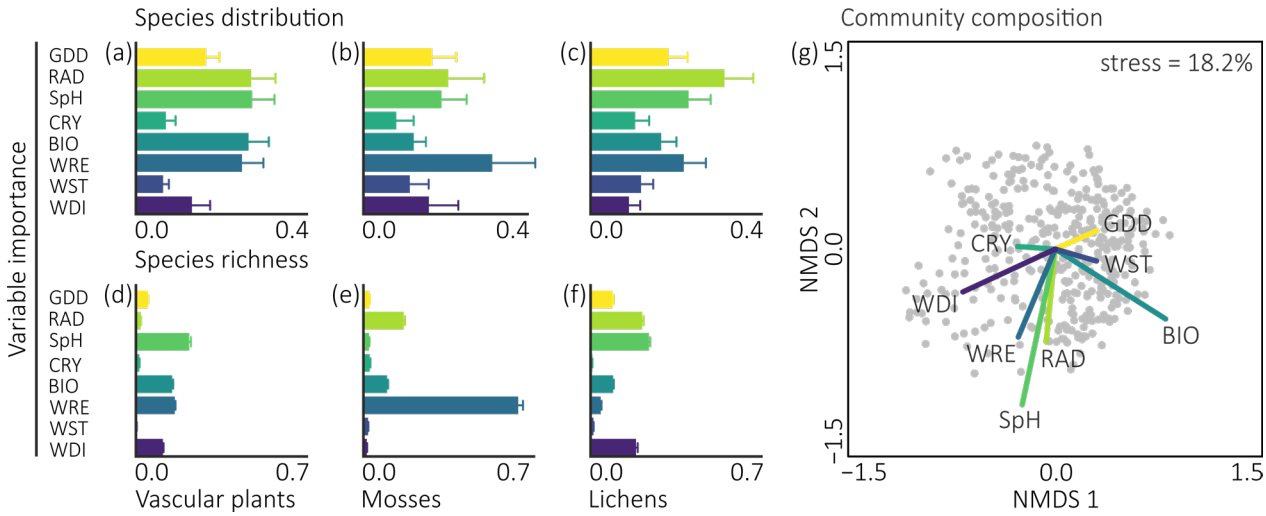


Figure 2. Variable importance (0.0 – 1.0) in models for species' distributions (a-c) and species richness (d-f) based on four modelling methods, and an ordination plot of community composition (g) (three dimensions; stress = 18.2%). Water resource (WRE) was the most important water-related variable for species distributions across all taxonomical groups (a-c), also showing the strongest overall influence on the occurrence of mosses (b). For species richness of mosses, the importance of WRE was exceptionally high, compared to all other predictors (e). Water disturbance (WDI) was the most influential water-related predictor for the species richness of lichens (f). Whiskers represent 95% confidence intervals. In the NMDS figure, the study plots are indicated by grey circles. Here, all three water-related predictors had independent influences on community composition (g; see Appendix S6 for this same plot, in which individual species are plotted. GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.

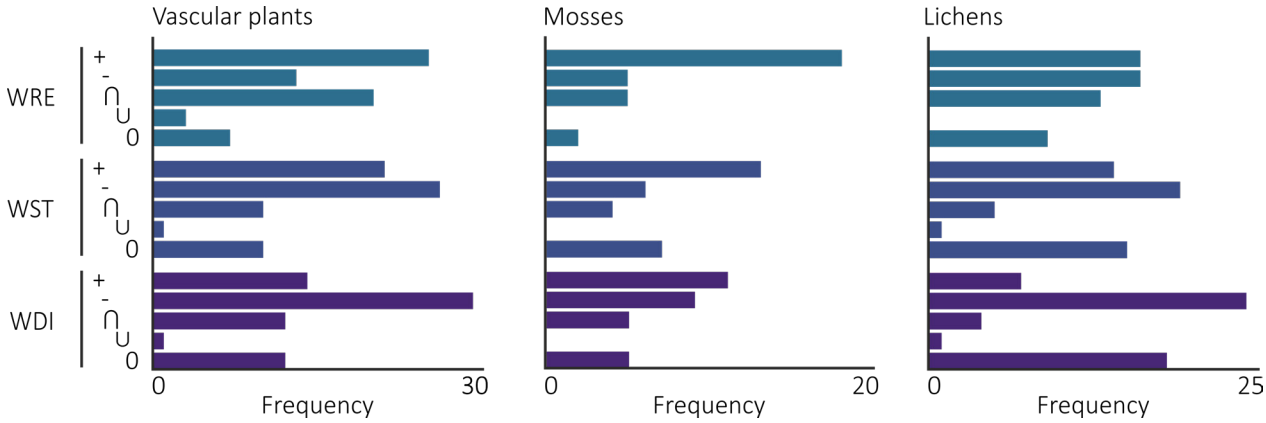


Figure 3. Responses of individual species to the water-related variables as modelled using generalized additive models. The responses vary between species groups, but also within each group, from positive (+) to negative (-) and from unimodal (∩) to bimodal (U) and no trend (0) responses. WRE = water resources; WST = water stress; WDI = water disturbance.

S4). For vascular plants, the AUC value increased from 0.807 to 0.836 (V = 1649.5, p = 0.004), for mosses from 0.687 to 0.727 (V = 324.0, p = 0.061), and lichens from 0.667 to 0.668 (V = 697.0, p = 0.698) (Appendix S4). In addition to WRE, RAD and SpH showed great influence in the distribution models (Figure 2 a-c).

Most vascular plant and moss species distributions responded positively to WRE, whereas lichen species distributions showed as many positive responses as negative ones (Figure 3). The majority of vascular plant and lichen species distributions responded negatively to WST and WDI, whereas for most moss species distributions the response to both WST and WDI was positive (Figure 3).

Species richness

WRE and WDI were strongly related to vascular plant species richness, with a contribution similar to RAD, SpH, and BIO (Figure 2 d-f). WRE was also important in moss richness models, clearly having the highest contribution in models of this response variable (Figure 2 e). In lichen richness models, WDI was the most influential water-related predictor after SpH and RAD (Figure 2 f). The predictive performance of all richness models improved significantly (two-tailed Wilcoxon signed rank test, $p \leq 0.001$), after including the water-related variables (Appendix S5). The R2 for the richness model based on all species increased from 0.250 to 0.332 (V = 31.0), for vascular plants from 0.427 to 0.568 (V = 1.0), for mosses from 0.097 to 0.193 (V = 1.0), and for lichens from 0.271 to 0.335 (V = 30.0) (for RMSE values, see Appendix S5).

In general, the relationship between WRE and vascular plant species richness was unimodal, whereas, for moss richness it was positive and for lichen richness negative (Figure 4). The relationship between WST and taxonomical groups showed similar patterns to WRE, with the exception of vascular plant species richness (negatively related to WST) (Figure 4). The relationship between WDI and vascular plant

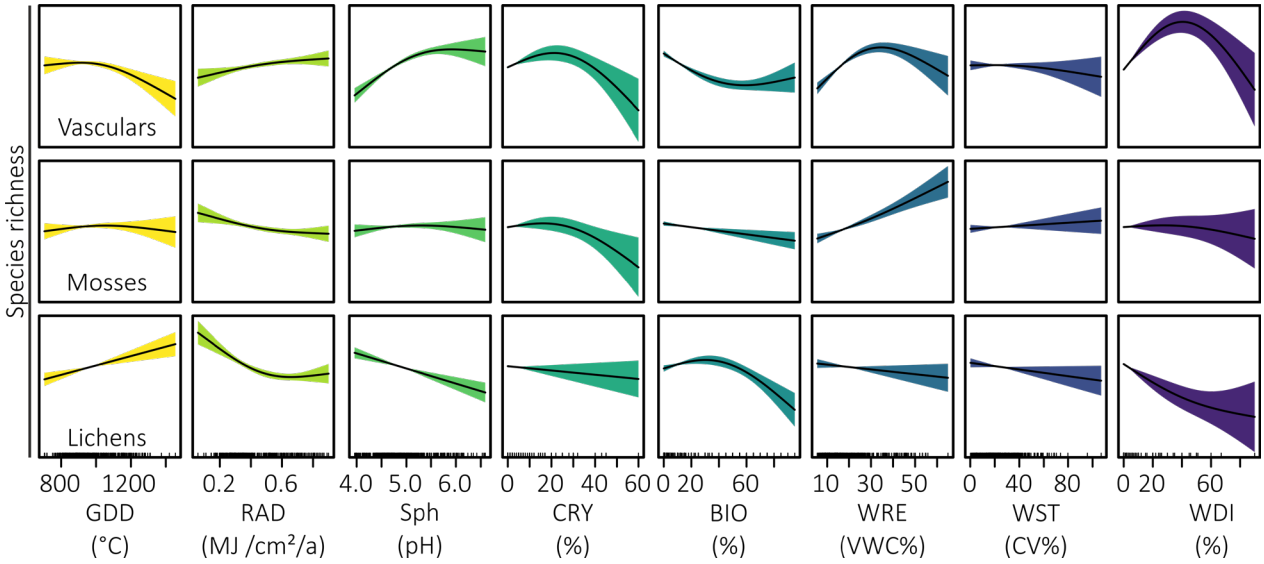


Figure 4. Relationships between species richness and the predictors, presented as generalized additive model response curves. All taxonomical groups have distinct response to the three water-related predictors. The shaded areas represent the 95% confidence intervals. GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.

species richness was unimodal, whereas for mosses and lichens it was negative (Figure 4).

Community composition

Community composition was significantly correlated with all the predictors ($p \leq 0.01$) (Figure 2 g; Appendix S6). SpH and BIO were the variables most strongly related to community composition ($R^2 = 0.506$ and 0.310 respectively), followed by two water variables: WDI and WRE ($R^2 = 0.208$ and 0.183, respectively) (Appendix S6; see also Appendix S7 for species-specific information).

Species-specific WRE and GDD optima

As WRE proved to be the most important water variable (Figure 2 a-c), it was chosen for further analysis (Figure 5). The influence of GDD and WRE on the distribution of species, variation in species richness and community composition showed diverse patterns across the three taxonomical groups (Figure 5). Distribution optima of vascular plant species spanned a broad range of WRE values (c. 10 – 50 VWC%), but covered only partially the GDD gradient (c. 800 – 1000°C) (Figure 5 a). Moss distribution optima showed a similar pattern (Figure 5 b), but optima for lichen distribution was more limited in WRE (c. 10 – 20 VWC%) and in GDD (c. 900 – 1000°C, respectively) (Figure 5 c). Vascular plant species richness was highest at c. 20 – 50 VWC% and with GDD < 1100°C (Figure 5 d). Mosses showed a different pattern, as their richness increased along the WRE gradient showing no response to GDD (Figure 5 e). Lichen species richness was the opposite: it increased with GDD and showed no response to WRE (Figure 5 f). Vascular plant communities in high GDD conditions were strongly correlated with the NMDS1 and were very different from communities in intermediate WRE conditions (Figure 5 g). In contrast, for moss communities, GDD conditions determined the differences between communities (Figure 5 h). Lichen communities differed strongly between high WRE with low GDD conditions and in low WRE and high GDD (Figure 5 I; see Appendix S8 forspecies-specific information).

Discussion

Here, we examined the roles of water-related factors in shaping fine-scale tundra vegetation patterns. Despite water being a vital resource for plants, its impact on vegetation has long been underestimated and overlooked (Silvertown et al. 2015), especially in studies regarding Arctic and alpine areas (Crimmins et al. 2011, le Roux et al. 2013a). Spatial and temporal variation in soil moisture and the intensity of fluvial disturbance were shown to be independent water-related aspects shaping species assemblages, even when controlling for the influences of other key environmental gradients (including, e.g., temperature and soil pH). These different water aspects have crucial impacts on the distribution of individual species, patterns of species richness, and community composition of vascular plants, mosses, and lichens.

In light of rising temperatures, particularly in high altitude systems, vascular plant patterns are likely to become more dependent on hydrological conditions (Crimmins et al. 2011, Winkler et al. 2016). Indeed, for high-latitude vegetation, soil moisture may mediate the impacts of changing climatic conditions, including rising temperature and changing snow dynamics (Nabe-Nielsen et al. 2017). Thus, hydrological refugias may occur in high-latitudes, sustaining suitable environmental conditions for threatened species and vegetation types (McLaughlin et al. 2017). However, the future changes in the tundra water cycle and its altered seasonality could

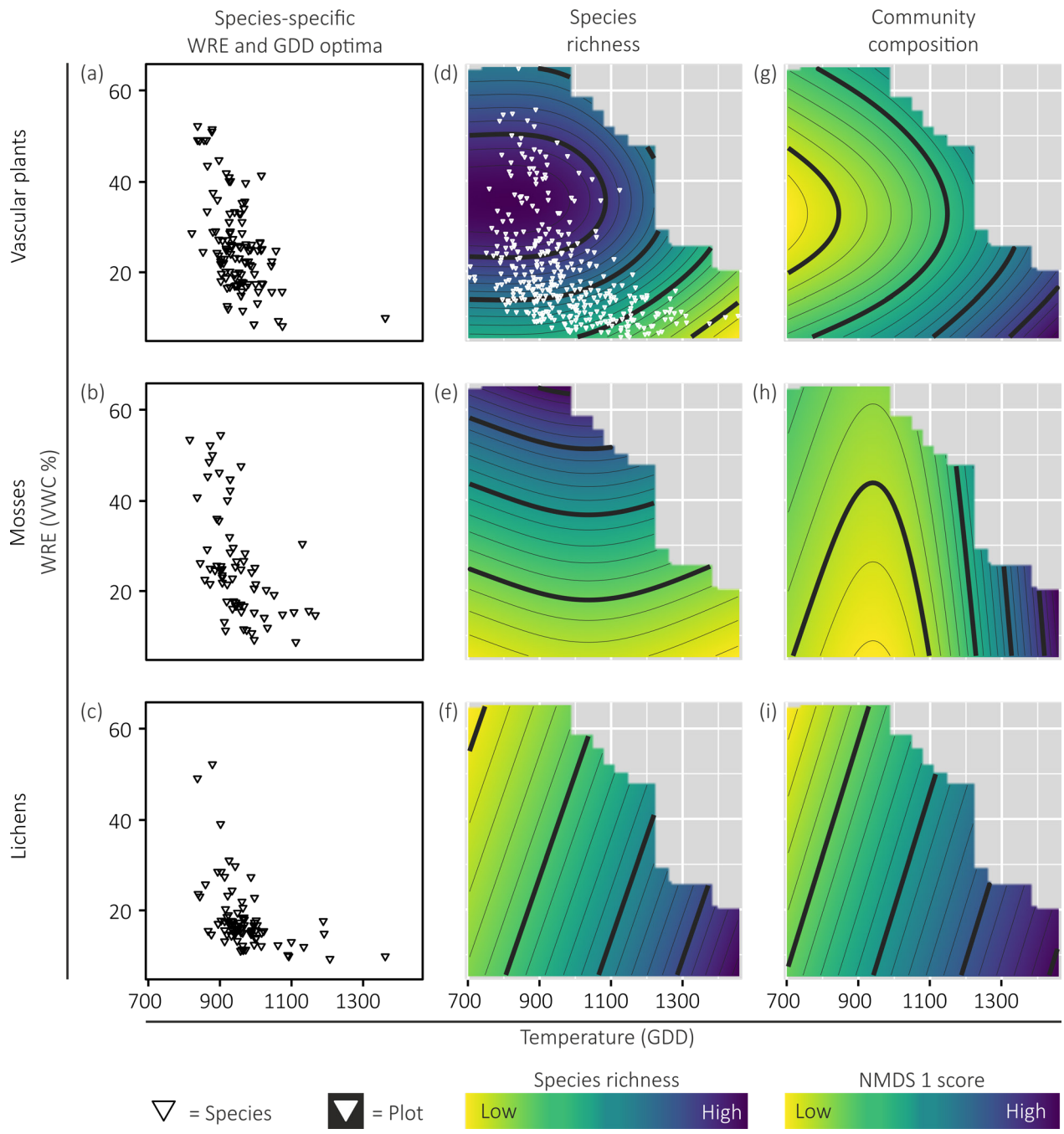


Figure 5. Species-specific water resource (WRE) and temperature (GDD) optima (a-c), and predictions of species richness (d-f) and community composition (g-i) optima in relation to WRE and GDD. Here, species-specific WRE and GDD optima are defined as the median distribution of each species along the WRE and GDD gradients. Species-specific optima shows that vascular plant and moss species exhibits a wide range of WRE optima and a narrow range of GDD optima (a-b). In contrast, optima for lichen species distribution is broader for GDD than for WRE. Prediction of species richness optima revealed that vascular plants chiefly prefer specific (intermediate) GDD conditions, but are more varied with WRE (d). For mosses, high species richness is strongly correlated with high WRE conditions (e), whereas with high GDD for lichens. The community composition optima was based on the scores of the first NMDS axis (Figure 2 g). Vascular plant communities under high GDD conditions are highly correlated with NMDS1 scores, but are very different from communities in intermediate WRE conditions (g). In contrast, for moss community composition, GDD conditions determine the differences between communities. Lichen communities differ strongly between conditions of high WRE with low GDD conditions and in low WRE and high GDD. Triangles with black borders (a-c) represent individual species and white triangles (d) measured plots. GDD = growing degree day; WRE = water resources (measured as mean soil moisture).

eliminate several hydrologically distinct habitats in high-latitude environments, including meltwater streams and snowbeds (Bintanja and Andry 2017, Franklin et al. 2016), which may consequently eliminate a portion of the tundra species pool (Niittynen et al. 2018). It can be particularly challenging to predict the impact of climate change impacts on plant-available water, as soil moisture conditions may not reflect the prevailing microclimate, which may, in turn, be highly decoupled from the macroclimate (Aalto et al. 2018). Therefore, it is critical to focus future research on quantifying plant-available water resources, and stresses, and disturbances related to water at ecologically relevant spatial and temporal scales.

Our results provide evidence on the pivotal role of water in shaping fine-scale spatial patterns of tundra vegetation: species have individual responses and distinct optima to

different water aspects. The strong contribution of the water variables in our distribution models and response shapes show that tundra vegetation has species-specific hydrological niches. As water is a key factor for all vegetation, hydrological niche segregation (HNS) occurs in various vegetation types, wherever competing species co-exist, not only in water-limited systems (Silvertown et al. 2015). HNS was evident regarding the diverse responses to water-aspects of our study species within each taxonomic group: all species have a unique response to different water aspects. In general, tundra vascular plants are adapted to a wide range of water conditions, as well as, typically, to relatively low temperatures and a short growing-season. Whereas, the majority of mosses occur in wet conditions regardless of temperature conditions, while lichens show the opposite tendency. Thus, the spatial heterogeneity of tundra water conditions together with other environmental factors, such as temperature, enable the co-occurrence of eco-physiologically distinct species (and higher taxonomic groups), which increases the overall species diversity in tundra (Whittaker 1972). Consequently, instead of focusing on regional averages, more research is needed on local hydrological heterogeneity in the tundra, and how this fine-scale variability in water conditions will be affected in tundra under a changing climate.

Water as a resource proved to be the most important water aspect for the three taxonomic groups. Due to the distinct life histories and physiology of the three taxonomical groups, they have different adaptations to cope with local water conditions (Iturrate-Garcia et al. 2016). Generally, vascular plants are stronger competitors than mosses, but in both extremes of the soil moisture gradient, these roles may be reversed (Iturrate-Garcia et al. 2016). For example, mosses dominate in nearly water-logged conditions, in which the roots of vascular plants may suffer from anoxic conditions. Moreover, lichens and mosses are more tolerant than vascular plants of soil instability in wet environments (e.g. cryoturbation habitats; le Roux et al. 2014a), due to the lack of a root system, which predisposes vascular plants to damage from mechanical disturbance (Jonasson 1986). However, when soil moisture is low, roots enable better access to soil moisture. Nevertheless, in the driest extreme of the moisture gradient, even extensive roots may not provide sufficient amounts of water for high-demanding vascular plants, thus, only desiccation-tolerant lichen and moss species can survive there.

The changing tundra hydrology may permanently alter entire ecosystems by reshuffling species communities. This is due to the different functional roles of the three taxonomic groups and their diverse responses to different water aspects demonstrated in our results. For example Arctic greening (i.e. shrub encroachment and shrubification) may be exacerbated by changes in local factors, such as soil moisture conditions (Weijers et al. 2018). Indeed, soil moisture is known to impact climate sensitivity of shrub growth, and may therefore mediate how shrub growth responds to warming temperatures (Myers-Smith et al. 2015). Arctic browning (i.e. experiencing plant dieback) is also linked to wetter and warmer climatic conditions (Epstein et al. 2016, Lara et al. 2018). Due to the reduction of photosynthesis during increased water stress (Angert et al. 2005), extreme weather events, such as droughts, may lead to "browning" as well (Bjerke et al. 2017, Phoenix and Bjerke 2016). The expansion of vascular plants and mosses causes population declines in lichens, however, due to lichen species' higher tolerance to, e.g. desiccation, extreme conditions may compensate or reverse population declines (Bjerke et al. 2011). This further demonstrates that future vegetation predictions must take into consideration not only the level of plant-available water, but also temporal variability in fine-scale hydrological conditions, which may lead to water stress and disturbance.

Water stress had relatively minor effect on species occurrences. Our water stress factor, based on three measurements over one growing season, could benefit from a more intensive moisture survey (e.g. hourly measurements) or another type of approach (e.g. relative water content of leaves) that could have shown higher significance of water stress over tundra vegetation (Buckland et al. 1997, Dolezal et al. 2016). Thus, our findings call for incorporating temporally comprehensive measurements over the growing season for capturing the entire spectrum of water conditions of extreme stress to stable conditions. Despite these data limitations, our results are highly promising and stress the need of more research on the different aspects affecting tundra ecohydrology.Our results highlight the essential role of water as a multifaceted driver of tundra vegetation, where in general, water resources are not scarce. In global change context, these fundamental elements of Arctic ecosystems, namely vascular plant, moss, and lichen communities, will not only show sensitivity to warming temperatures, but they will also respond to altered water conditions. The changing Arctic hydrology can have pronounced and differing consequences for the three taxonomical groups, which may potentially cascade on other trophic levels and processes as well (Callaghan et al. 2004, Porazinska et al. 2018, Post et al. 2009). Due to uncertainties in projecting future hydrological cycles (Bring et al. 2016), there are possibly ecological surprises ahead for high-latitude ecosystems. Thus, water and its multiple aspects should be considered in future climate change impact assessments.

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Author contributions

All authors contributed to the original idea, data collection and manuscript preparation. Study design by PCleR, ML and JA, analysis and visualization by JK and PN.

Conflicts of interest

The authors declare no conflicts of interest.

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Supplementary material Appendix 1. Notes on species identification and species list.

We identified all species at species level, except those that cannot be reliably identified (*Alchemilla* spp., *Taraxacum* spp., *Cladonia chlorophaea* section, *Lepraria* spp.). We included the most abundant liverworth (*Ptilidium ciliare*) in moss species. We excluded mosses and lichens that grow on rock surfaces, because they are affected by other environmental variables. We followed the taxonomy of Hämet-Ahti et al. (1998) for vascular plants, Laine et al. (2011), Hallinbäck et al. (2006, 2008), and Hedenäs and Hallinbäck (2014) for mosses, and Stenroos et al. (2011) for lichens.

Hallinbäck T. et al. 2006. Nationalnyckeln till Sveriges flora och fauna. Bladmossor: sködmossor–blåmossor. Bryophyta: Buxbaumia–Leucobryum. – ArtDatabanken, SLU.

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Hämet-Ahti L. et al. 1998. Retkeilykasvio (Field Flora of Finland). – Finnish Museum of Natural History, Botanical Museum.

Laine J. et al. 2011. The intricate beauty of Sphagnum mosses – a finnish guide to identification. – Univ. of Helsinki, Dept of Forest Sciences.

Stenroos S. et al. 2011. Suomen jäkäläopas. – Luonnontieteellisen keskusmuseon kasvimuseo.

The species list contains species with ≥ 8 observations, all together 153 species (69 vascular plant, 30 moss, and 54 lichen species), of which *Empetrum hermaphoditum* was used as a predictor.

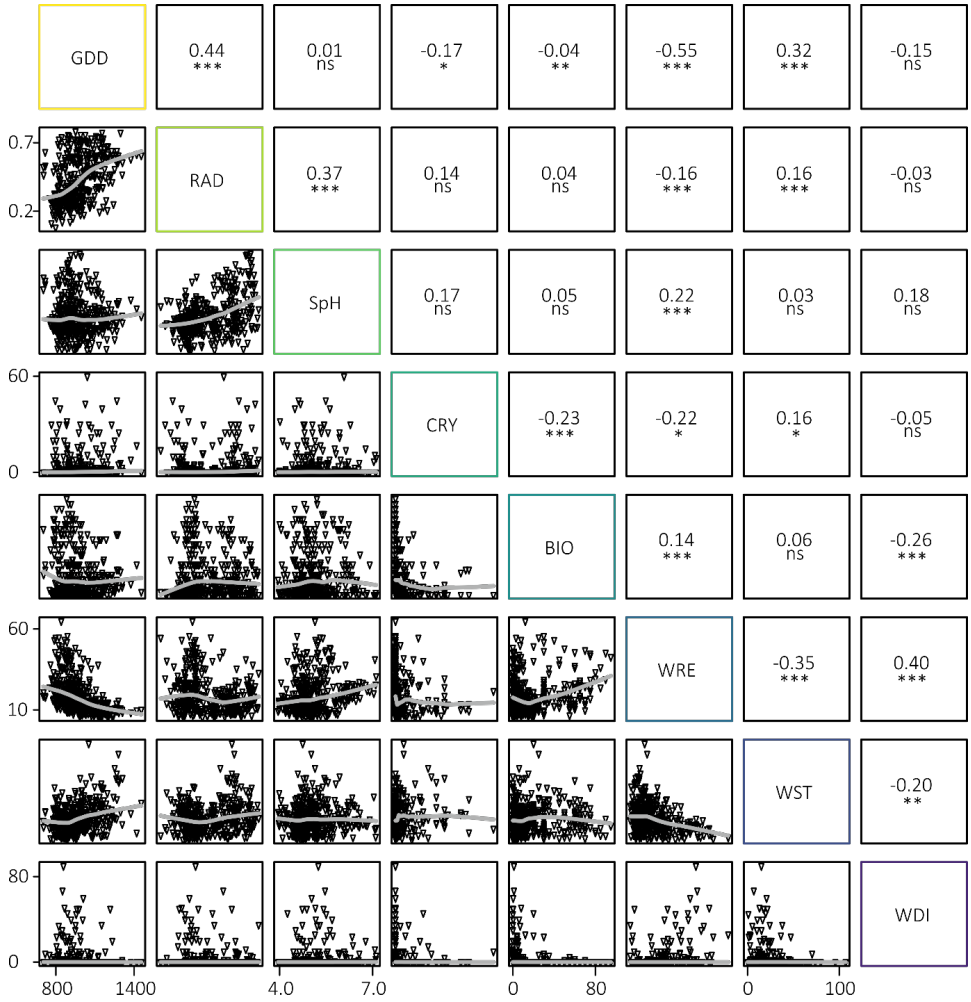
Abbraviation	Species name	Taxonomical group	Observations
VACVIT	*Vaccinium vitis-idaea*	Vascular plant	344
EMPHER	*Empetrum hermaphroditum*	Vascular plant	335
BETNAN	*Betula nana*	Vascular plant	278
CLAMIT	*Cladonia mitis*	Lichen	257
FESOVI	*Festuca ovina*	Vascular plant	246
CARBIG	*Carex bigelowii*	Vascular plant	215
CETERI	*Cetraria ericetorum*	Lichen	205
FLACUC	*Flavocetraria cucullata*	Lichen	203
DICSCO	*Dicranum scoparium*	Moss	195
POLJUN	*Polytrichum juniperinum*	Moss	191
VACULI	*Vaccinium uliginosum*	Vascular plant	183
PTICIL	*Ptilidium ciliare*	Liverworth	179
CLAPLE	*Cladonia pleurota*	Lichen	178
DICELO	*Dicranum elongatum*	Moss	175
STEALP	*Stereocaulon alpinum*	Lichen	169
DICFUS	*Dicranum fuscescens*	Moss	169
CLAUNC	*Cladonia uncialis*	Lichen	160
BISVIV	*Bistorta vivipara*	Vascular plant	159
CLAMAX	*Cladonia maxima*	Lichen	152
CALLAP	*Calamagrostis lapponica*	Vascular plant	147
SALHER	*Salix herbacea*	Vascular plant	144
SOLVIR	*Solidago virgaurea*	Vascular plant	143
HYLSPL	*Hylocomium splendens*	Moss	135
PHYCAE	*Phyllodoce caerulea*	Vascular plant	133
PARAMB	*Parmeliopsis ambigua*	Lichen	133
VACMYR	*Vaccinium myrtillus*	Vascular plant	132
LINBOR	*Linnaea borealis*	Vascular plant	129
CLAGRA	*Cladonia gracilis*	Lichen	129
CETSEP	*Cetraria sepincola*	Lichen	126
OCHFRI	*Ochrolechia frigida*	Lichen	125
JUNTRF	*Juncus trifidus*	Vascular plant	125
POLPIL	*Polytrichum piliferum*	Moss	120
POHNUT	*Pohlia nutans*	Moss	119
DESFLE	*Deschampsia flexuosa*	Vascular plant	116
FLANIV	*Flavocetraria nivalis*	Lichen	112
PLESCH	*Pleurotzium schreberi*	Moss	105
PEDLAP	*Pedicularis lapponica*	Vascular plant	104
PARHYP	*Parmeliopsis hyperopta*	Lichen	100
HIERAC	*Hieracium* spp.	Vascular plant	97
HYPPHY	*Hypogymnia physodes*	Lichen	95
CLACHL	*Cladonia chlorophaea*	Lichen	95
CLARAN	*Cladonia rangiferina*	Lichen	91
SPHGLA	*Sphaerophorus globosus*	Lichen	79
CLABEL	*Cladonia bellidiflora*	Lichen	76
THAVER	*Thamnolia vermicularis*	Lichen	74
BRYDIV	*Bryocaulon divergens*	Lichen	74
PELSCA	*Peltigera scabrosa*	Lichen	72
LEPSP	*Lepraria* spp.	Lichen	72
VIOBIF	*Viola biflora*	Vascular plant	71
JUNICO	*Juniperus communis*	Vascular plant	70
PELAPH	*Peltigera aphthosa*	Lichen	69
CETISL	*Cetraria islandica* ssp. *islandica*	Lichen	69
ASTALP	*Astragalus alpinus*	Vascular plant	68
ARCALP	*Arctostaphylos alpina*	Vascular plant	68
GOWNIG	*Gowardia nigricans*	Lichen	67
CLAFIM	*Cladonia fimbriata*	Lichen	66
CLAARB	*Cladonia arbuscula*	Lichen	61
SAUALP	*Saussurea alpina*	Vascular plant	58
POLHYP	*Polytrichum hyperboreum*	Moss	57
ANTALP	*Antennaria alpina*	Vascular plant	57
NEPARC	*Nephroma arcticum*	Lichen	56
SOLCRO	*Solorina crocea*	Lichen	54
LYCALP	*Lycopodium annotinum*	Vascular plant	51
RHYRUG	*Rhytidium rugosum*	Moss	50
ANTXAL	*Anthoxanthum alpinum*	Vascular plant	50
THAALP	*Thalictrum alpinum*	Vascular plant	48
CASTET	*Cassiope tetragona*	Vascular plant	48
GNASUP	*Gnaphalium supinum*	Vascular plant	47
CLAAMA	*Cladonia amaurocrea*	Lichen	45
ALEOCH	*Alectoria ochroleuca*	Lichen	43
EQUSCI	*Equisetum scirpoides*	Vascular plant	39
CLADEF	*Cladonia deformis*	Lichen	39
POTCRA	*Potentilla crantzii*	Vascular plant	38
CETCRI	*Cetraria islandica* ssp. *crispiformis*	Lichen	38
DIPALP	*Diphasiastrum alpinum*	Vascular plant	37
CARVAG	*Carex vaginata*	Vascular plant	37
CARRUP	*Carex rupestris*	Vascular plant	36

Abbraviation	Species name	Taxonomical group	Observations
PSOHYP	*Psoroma hypnorum*	Lichen	35
POLLON	*Polytrichum longisetum*	Moss	34
POAALP	*Poa alpina*	Vascular plant	34
DIALAP	*Diapensia lapponica*	Vascular plant	34
CASHYP	*Cassiope hypnoides*	Vascular plant	34
PELMAL	*Peltigera malacea*	Lichen	33
SIBPRO	*Sibbaldia procumbens*	Vascular plant	32
DICMAJ	*Dicranum majus*	Moss	32
CAMROT	*Campanula rotundifolia*	Vascular plant	32
HIEALP	*Hierochloë alpina*	Vascular plant	31
ARCUVA	*Arctostaphylos uva-ursi*	Vascular plant	31
TRIEUR	*Trientalis europaea*	Vascular plant	29
BARALP	*Bartsia alpina*	Vascular plant	29
RANACR	*Ranunculus acris*	Vascular plant	28
VERALP	*Veronica alpina*	Vascular plant	27
SALMYD	*Salix myrtilloides*	Vascular plant	27
HUPARC	*Huperzia selago*	Vascular plant	27
CETNIG	*Cetraria nigricans*	Lichen	27
PELRUF	*Peltigera rufescens*	Lichen	26
DRYOCT	*Dryas octopetala*	Vascular plant	26
DICCRI	*Dicranoweisia crispula*	Moss	25
POLALP	*Polytrichastrum alpinum*	Moss	24
TARSPP	*Taraxacum* spp.	Vascular plant	23
SILACA	*Silene acaulis*	Vascular plant	23
SANUNC	*Sanionia uncinata*	Moss	23
SALGLA	*Salix glauca*	Vascular plant	23
LUZCON	*Luzula confusa*	Vascular plant	22
CLABOR	*Cladonia borealis*	Lichen	22
CETDEL	*Cetrariella delisei*	Lichen	22
ANTDIO	*Antennaria dioica*	Vascular plant	22
STECUM	*Stereocaulon cumulatum*	Lichen	21
PYRMIN	*Pyrola minor*	Vascular plant	21
CNEALP	*Cnestrum alpestre*	Moss	21
SELSEL	*Selaginella selaginoides*	Vascular plant	20
ANDRUP	*Andreae rupestris*	Moss	20
RACLAN	*Racomitrium lanuginosum*	Moss	17
POLCOM	*Polytrichum commune*	Moss	17
PELCAN	*Peltigera canina*	Lichen	17
EQUPRA	*Equisetum pratense*	Vascular plant	17
CLASUL	*Cladonia sulphurina*	Lichen	17
RHIPSE	*Rhizomnium pseudopunctatum*	Moss	16
MNIBLY	*Mnium blyttii*	Moss	15
LOIPRO	*Loiseleuria procumbens*	Vascular plant	15
ICMERI	*Icmadophila ericetorum*	Lichen	15
CLATRA	*Cladonia trassii*	Lichen	15
SALPOL	*Salix polaris*	Vascular plant	14
POHCRU	*Pohlia cruda*	Moss	14
CONTET	*Conostonum tetragonum*	Moss	14
SALHAS	*Salix hastata*	Vascular plant	13
GERSYL	*Geranium sylvaticum*	Vascular plant	13
CLACEN	*Cladonia cenotea*	Lichen	13
ANDPOL	*Andromeda polifolia*	Vascular plant	13
OCHSP	*Ochrolechia sp.*	Lichen	12
CLACAR	*Cladonia carneola*	Lichen	12
ANTCAN	*Antennaria canescens*	Vascular plant	12
ALESAR	*Alectoria sarmentosa*	Lichen	12
DRADAU	*Draba daurica*	Vascular plant	11
DICMON	*Dicranum montanum*	Moss	11
ALCHEM	*Alchemilla* spp.	Vascular plant	11
SPHCAP	*Sphagnum capillifolium*	Moss	10
MINBIF	*Minuartia biflora*	Vascular plant	10
EUPFRI	*Euphrasia frigida*	Vascular plant	10
CLAPYX	*Cladonia pyxidata*	Lichen	10
SCISTA	*Sciuro-hypnum starkei*	Moss	9
SALRET	*Salix reticulata*	Vascular plant	9
RHOROS	*Rhodiola rosea*	Vascular plant	9
POGDEN	*Pogonatum dentatum*	Moss	9
NEPPAR	*Nephroma parile*	Lichen	9
CLASUB	*Cladonia subulata*	Lichen	9
CLAMET	*Cladonia metacorallifera*	Lichen	9
AULTUR	*Aulacomnium turgidum*	Moss	9
NEPEXP	*Nephroma expallidum*	Lichen	8
LYCHAL	*Viscaria alpina*	Vascular plant	8
ERIUNI	*Erigeron uniflorus*	Vascular plant	8
CLASTR	*Cladonia stricta*	Lichen	8
BETCZE	*Betula pubescens*	Vascular plant	8

Supplementary material Appendix 2. Summary statistics of the predictors based on 378 observations, mean, standard deviation (Sd), and range, respectively.

Predictors	Units	Mean	Sd	Range
Growing degree day	°C	969.0	134.6	704.0 - 1455.0
Radiation	MJ/cm²/a	0.5	0.2	0.1 - 0.9
Soil pH	pH	4.9	0.5	4.0 - 6.6
Cryogenic processes	%	3.4	8.3	0.0 - 60.0
Biota	%	18.9	22.5	0.0 - 95.0
Water resources	VWC%	19.6	11.3	5.5 - 64.9
Water stress	CV%	24.7	15.9	0.2 - 107.0
Water disturbance	%	3.4	10.6	0.0 - 90.0

Supplementary material Appendix 3. Spearman correlations between predictors. The lowess lines (in grey) depict the locally fitted function. Statistical significance of the correlation: *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$; ns = $p \geq 0.05$. GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.



Supplementary material Appendix 4. Mean and standard error values (mean ± SE) for predictive performance of the species distribution models as assessed by the area under curve (AUC) and true skill statistics (TSS) (based on 100 cross-validation rounds). Statistical significance tested with Wilcoxon's paired rank test. Base model excludes the three water-related variables.

	AUC				TSS			
	Base model	Full model	V	p	Base model	Full model	V	p
All taxa	0.733 ± 0.010	0.754 ± 0.010	7241.0	0.009	0.462 ± 0.015	0.493 ± 0.016	7011.0	0.028
Vascular plants	0.807 ± 0.012	0.836 ± 0.011	1649.5	0.004	0.577 ± 0.021	0.622 ± 0.020	1596.0	0.010
Mosses	0.687 ± 0.019	0.727 ± 0.019	324.0	0.061	0.392 ± 0.027	0.434 ± 0.031	296.0	0.198
Lichens	0.667 ± 0.016	0.668 ± 0.016	697.0	0.698	0.357 ± 0.020	0.363 ± 0.022	697.5	0.702

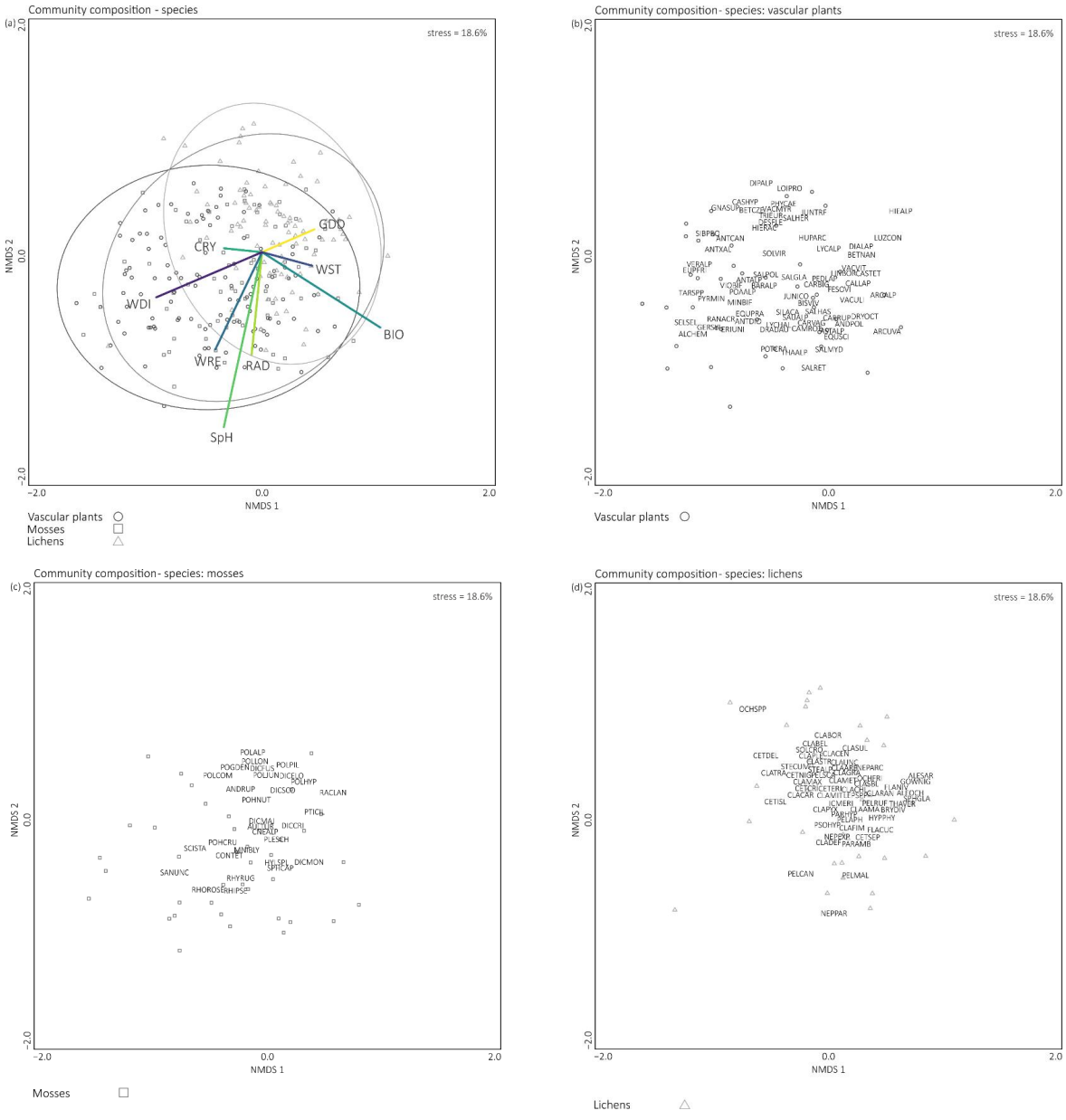
Supplementary material Appendix 5. Mean and standard error values (mean ± SE) for predictive performance of species richness models measured with the root mean squared error (RMSE) and coefficient of determination (R^2) (100 permutations). The results from a two-tailed Wilcoxon's paired rank test are shown comparing the base model (excludes the three water variables) and the full model.

	RMSE				R^2			
	Base model	Full model	V	p	Base model	Full model	V	p
All taxa	6.479 ± 0.049	6.128 ± 0.048	4999.0	< 0.001	0.250 ± 0.006	0.332 ± 0.007	31.0	< 0.001
Vascular plants	5.168 ± 0.037	4.507 ± 0.037	5009.0	< 0.001	0.427 ± 0.006	0.568 ± 0.007	1.0	< 0.001
Mosses	2.107 ± 0.014	1.999 ± 0.013	4999.0	< 0.001	0.097 ± 0.004	0.193 ± 0.005	1.0	< 0.001
Lichens	3.885 ± 0.026	3.714 ± 0.025	5026.0	< 0.001	0.271 ± 0.005	0.335 ± 0.005	30.0	< 0.001

Supplementary material Appendix 6. The relationship between predictor variables and community composition (as qualified by NMDS scores) of whole species community models (stress = 17.0%). GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.

	NMDS1	NMDS2	R^2	p
GDD	0.916	0.400	0.051	0.001
RAD	-0.102	-0.995	0.167	0.001
SpH	-0.213	-0.977	0.506	0.001
CRY	-0.995	0.102	0.023	0.008
BIO	0.843	-0.538	0.310	0.001
WRE	-0.433	-0.901	0.183	0.001
WST	0.965	-0.261	0.042	0.002
WDI	-0.920	-0.393	0.208	0.001

Supplementary material Appendix 7. Ordination plot of community composition (a), in which individual species are plotted in grey symbols (three dimensions; stress = 18.6%). For visualization, the same information is presented by dividing the first figure (a) according to taxonomic group (b-d). Vascular plant species were separated chiefly along NMDS1 and lichens species along NMDS2, with an intermediate pattern observed for mosses. Abbreviations for species name provided in Appendix S1. Only species present in ≥ 8 of the plots are indicated. Overlapping labels were slightly moved for readability. The ellipsoids represent the 95% confidence interval, with vascular plant species in dark grey, mosses in grey, and lichens in light grey (a).Vascular plant species are indicated with dark grey circles (a, b), mosses with grey squares (a, c), and lichens with light grey triangles (a, d). GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.



Supplementary material Appendix 8. Ordination plots of vascular plant, moss, and lichen community composition (a, c, e). In contrast to the ordinations in Appendix S7, here NMDS was used to perform ordination for each taxonomic group separately, highlighting the relative influence of predictor variables separately for each taxonomic group. Individual species are plotted in grey symbols. Abbreviations for species name provided in Appendix S1. Only species present in ≥ 8 of the plots are indicated. Overlapping labels were slightly moved for readability. Vascular plant species are indicated with dark grey circles (a, b), mosses with grey squares (c, d), and lichens with light grey triangles (e, f). GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.